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THE CHAÑARES (ARGENTINA) TRIASSIC REPTILE FAUNA

X. TWO NEW BUT INCOMPLETELY KNOWN LONG-LIMBED PSEUDOSUCHIANS.

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ABSTRACT. Two types of hind limbs, with which incomplete remains of other skeletal parts are associated, are described as new genera and species, *Lagerpeton chanarensis* and *Lagosuchus talampayensis*. Both have long and slender legs, with the tibia longer than the femur, and a long slender foot. They differ, however, in foot construction, for in *Lagerpeton* digit II is short and digit IV the longest of the series, whereas in *Lagosuchus* metatarsals II–IV are subequal in length and digit III the longest in the foot.

INTRODUCTION

In the pseudosuchian material collected by the La Plata-Harvard expedition of 1964–1965, there are several forms represented by nearly complete skeletal material. In addition, however, in this collection and among specimens collected later by Sr. Bonaparte of the Instituto Lillo of Tucumán, there are less complete remains of further pseudosuchians. Two such forms are represented by materials including hind limbs of unusual and advanced character; these will be described here.

LAGERPETON CHANARENSIS gen. et sp. nov.

Holotype. La Plata Museum No. 64–XI–14–10 (field number 64), a hind leg, collected from the Chañares Formation in La Rioja Province, Argentina, about 4½ miles east of the mouth of Río Chañares.

Combined generic and specific diagnosis. A pseudosuchian; hind limb very long and slender; femur with articular head sharply set off from shaft; tibia and fibula longer than femur; astragalus

and calcaneum fused and applied closely to tibia and fibula; toe IV longest of the hind leg digits; toe II much shorter than III or IV; toe V represented by short metatarsal only.

Description. The type specimen (Fig. 1) was found quite isolated, not articulated with or accompanied by other skeletal materials. The femur is long and slender, with a length of 77 mm. It has the typical sigmoidal archosaur shape. The well-ossified curved articular area of the head is pronounced and set off at a sharp angle from the shaft. A marked angulation of the posterior

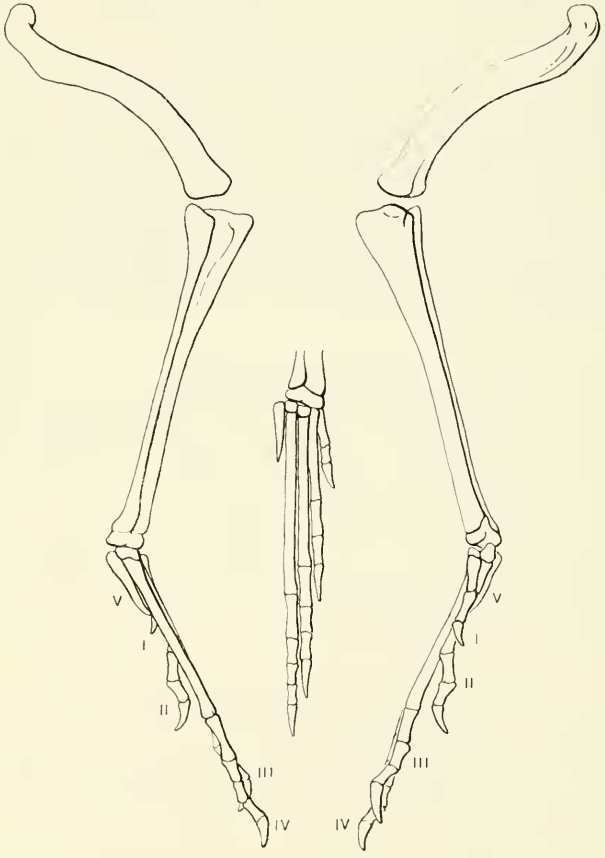

Figure 1. Right hind leg of *Lagerpeton,* holotype. Left, external view; center, extensor surface of foot; right, internal view. × 1/2.

margin of the shaft indicates the point of insertion of musculature, presumably the iliofemoralis. On the medial surface below the head, there is a well-developed fourth trochanter in the shape of a pronounced ridge, presumably for the insertion of the caudifemoralis.

The epipodials are even more elongate and slender than the femur; the tibia measures 92 mm in length, and is thus about 120 per cent the length of the femur. The tibia is well expanded proximally for a broad double articulation with the distal end of the femur. The fibula is incomplete in the type, and I have in my figure restored the proximal end from a specimen, discussed below, in the Instituto Lillo collection. It is, as always, a slender strap of bone expanded at either end; proximally, it articulates with the lateral surface of the distal end of the femur.

The proximal tarsals are of unusual construction for a thecodont. Astragalus and calcaneum are completely fused in the type specimen; in their combined outline they conform to the area of the distal end of tibia plus fibula, and this astragalo-calcaneum is closely applied to these two elements, although not fused with them. Further contributing to the close union of the astragalo-calcaneum with the epipodials is a triangular flange of bone extending upward from this element posteriorly over the lower ends of tibia and fibula. There is here no indication of the crocodiloid calcaneal tuber frequently found in pseudosuchians.

The usual two distal tarsals are present. A more medial and larger element is present on the ventral surface, above the third metatarsal; the lateral element caps metatarsal IV.

Like the main limb elements, the foot is long and slender, the toes apparently lying close together in life. Toe V is represented only by a short, pointed metapodial; the other toes are complete, with the primitive phalangeal formula of 2, 3, 4, 5. The terminal phalanges of toes I–IV are sharp claws, somewhat curved. Most unusual for an archosaur, the toes are primitive in one regard, namely that toe IV is the longest of the series. Digit I is, as often, short; digit II is also shortened, its metapodial having but about half the length of those of its lateral neighbors. The total lengths of the digits, from toe I outward, are 21, 49, 69, 85, and 18 mm. Metapodial lengths are 8, 24, 45, 48, and 18 mm.

In the Instituto Lillo collections is a specimen that includes a hind leg similar to that of the type in size, bone proportions, and

structure. The femur is 75 mm in length, the tibia (not perfectly preserved) about 90 mm. The femur is closely comparable to that of the type with its sharply set off head and prominent trochanteric ridge. Toe I is not preserved, but toes II–IV resemble closely those of the type, with metapodial lengths of 23, 42, and 47 mm, and total toe lengths of 48, 74, and 87 mm.

With this specimen is a pelvis which is apparently nearly complete, but in its present state of preparation is seen only from its ventral aspect. The ischia are well developed and extend far backward with a long symphysis. Below and somewhat to the rear of the level of the acetabulum their broad external surfaces are convex in section, giving this region a "swollen" appearance.

Lagosuchus talampayensis gen. et sp. nov.

Holotype. La Plata Museum No. 64–XI–14–11 (in part). Remains included in a slab collected from the Chañares Formation in La Rioja Province, Argentina, about 2 km north of the mouth of Río Chañares.

Combined generic and specific diagnosis. A pseudosuchian; hind limb similar in many regards to that of *Lagerpeton;* limb long and slender; femur with articular head sharply set off from shaft; tibia and fibula longer than femur; astragalus and calcaneum fused and applied closely to tibia and fibula. Digit I short, digit V represented by short metatarsal only; digits II–IV subequal in metatarsal length, but digit III longest of the series.

Description. A slab from the Chañares exhibits on one surface the greater part of the skeleton of a small ornithosuchid which I hope to describe in a later number of this series. On the other surface of the slab are scattered materials pertaining to a still smaller pseudosuchian. Best preserved are nearly complete and articulated hind limbs (Fig. 2). Although considerably smaller, these limbs in their proportions resemble those of *Lagerpeton,* and I at first assumed that the specimen was an immature individual of that genus. The foot structure, however, shows that we are dealing with a discrete form of smaller size.

As in *Lagerpeton,* the limbs are long and slender; the head of the femur is set off sharply from the shaft and the trochanteric ridge is well developed. As in *Lagerpeton* the lower leg is longer than the femur, the two femora, as preserved, having lengths of 38 and 39 mm, the associated tibiae 47 and approximately 48 mm.

Figure 2. Hind foot of *Lagosuchus,* in ventral view. Composite of type and a specimen in the Instituto Lillo. 1 1/2 × size of holotype.

The proximal tarsal region is poorly preserved in the type. Two well-developed distal tarsals are present. Of the right foot, only metapodials, incomplete distally, are visible. The left foot is well preserved as regards the metatarsals and a portion of the phalanges. The digits are elongate and slender; metapodials II–IV are, as preserved, parallel to one another and closely apposed. Digit I, with a metapodial length of 15 mm, is short; metapodials II–IV have lengths of 23, 26, and 25 mm; metapodial V, broad at its head, tapers, as preserved, to a point at 11 mm. The two phalanges appropriate to digit I are present, as are single proximal phalanges articulated with metatarsals II and III, and several disarticulated phalanges (one a clawed ungual).

Scattered about the slab are disconnected series of vertebrae with average lengths of centra of 7.5 mm in the best preserved

region. There are, further, remains of pectoral limbs. In the better preserved of these the humerus has a length of 26 mm, the radius 16 mm. As one might expect from the nature of the long hind legs, the front limbs thus appear to be much reduced in size, the combined length of the long bones of the "arm" being less than half that of the corresponding hind leg elements.

A specimen in the Instituto Lillo collection includes much of the posterior part of a skeleton that is closely comparable to the type of *Lagosuchus* except for somewhat larger size. Much of both hind legs is preserved in articulation. Right and left femora measure 55 and 56 mm in length, the tibiae 72 and 70 mm.

As in *Lagerpeton,* astragalus and calcaneum are united and closely applied to tibia and fibula. Here, however, the line of suture between the two proximal tarsals is still visible, and a small spur of bone (not seen in *Lagerpeton*) projects backward from the fibular edge of the astragalo-calcaneum. There is no proximal extension of the astragalo-calcaneum of the sort seen in *Lagerpeton.* The two distal tarsals are present lying above the metatarsal heads.

The feet are incompletely preserved, but except for somewhat larger size, they compare well with those of the type. On the right foot metatarsals II and IV have lengths of 34 and 38 mm, respectively; lengths of metatarsals I–IV on the left foot are: 23, 35, 39, and 38 mm. No phalanges are present on metatarsal I, but two phalanges, with lengths of 9 and 7 mm are present on the second digit, three phalanges with lengths of 12, 8, and 5 mm on digit III, and four phalanges with lengths of 6, 5, 4, and 4 mm on digit IV. Metatarsal V, broad at the base and tapering distally, is incomplete, with a length as preserved of 10 mm.

In Figure 2 the foot is restored as a composite of the type and the Instituto Lillo specimen just described, with allowance made for the difference in size of the two specimens. The more distal phalanges are restored on digits II–IV. As restored, digital lengths of the Instituto Lillo specimen are, from digit I outward: 36, 56, 69, and 62 mm. Here, in contrast to *Lagerpeton,* there has developed the "typical" archosaur foot, with toe I relatively short, toe V reduced, and toe III the longest of the II–III–IV series.

Associated are remains of the pelvic girdle. The acetabula (into which the femoral heads were inserted when the specimen was recovered) are small and deep, strongly overhung dorsally by

the iliac rim. The acetabular construction plus the nature of the femoral head indicate rather surely that the femur moved in a fore-and-aft plane close to the body. The ilium (Fig. 3) is of peculiar structure. Above the acetabulum it constricts to a relatively narrow neck. Here there projects anterolaterally a short but stout, blunt-ended process of a sort otherwise unknown to me; it is possible that it afforded an origin for an iliofemoralis externus muscle as in the case of a somewhat similar process in some ornithischians (cf. Romer, 1927) and *Poposaurus* (Colbert,

Figure 3. Right ilium and head of femur of *Lagosuchus;* external process on ilium restored from left side. From a specimen in the Instituto Lillo. × 4/3.

1961). Above the "neck," the ilium expands to form a short blade. In all "normal" thecodonts the iliac blade is a simple single vertical structure; here, however, there lies, internal to the normal external blade, a broad trough, comparable to that seen in ophiacodonts, presumably for accommodation of dorsal axial muscles. Shallow posteriorly, this trough deepens and broadens anteriorly. Medial to this trough is a second iliac blade, tilted somewhat medially, to the inner surface of which the sacral ribs presumably articulated. Lateral and medial blades join anteriorly, closing the dorsal trough at this end. I know of such an iliac "trough" structure in only one other archosaur. In *Hesperosuchus,* Colbert (1952) found in the pelvic region an element which should have been an ilium but which, because of its peculiar nature, he concluded could not be that element. Its main peculiarity is its possession of a dorsal "trough" comparable to that of *Lagosuchus.*

Parts of pubis and ischium are present in this specimen. It is

clear that both pubis and ischium take part in the acetabulum, but in default of a better preserved specimen I refrain from discussion of this portion of the girdle.

Found close to the limbs and pelvic remains were two series of vertebrae. One appears to include sacrals, followed by nine proximal caudals. The mean length of these caudal centra is approximately 7 mm. A first chevron is present between caudals three and four; its length is 13.5 mm; those following decrease in length, the fourth of the series measuring 10 mm. A second series of vertebrae includes 30 segments, apparently running to the tip of the tail. The first dozen, poorly preserved, appear to have a mean length of centra of about 7 mm; more posteriorly, the length increases to about 1 cm per segment. Chevrons, gradually decreasing in length to a nubbin, are present, as preserved, to a position between the tenth and eleventh from the end of the series.

A further Instituto Lillo specimen that may pertain to *Lagosuchus* includes an imperfect pelvis and much of the hind legs. As in both genera described in the present paper, the tibia is longer than the femur, with measurements of the right leg elements of 48 and 42 mm, respectively. As in *Lagosuchus,* metatarsals II–IV are subequal in length, with measurements of 24, 28, and 27 mm for these metapodials in the left foot. Possibly associated is a fragment of maxilla or dentary bearing small teeth spaced a bit more than a millimeter apart. A number of posterior dorsal vertebrae are present, with an average central length of 5.5 mm and a height of 7.5 to 8 mm.

DISCUSSION

So distinctive are the hind legs which are the major preserved portions of the two forms described above that formal systematic description of them seems justified despite the paucity of further associated anatomical structures. Greater length of tibia than of femur is generally regarded as associated with speed. Greater length of lower leg than thigh is present in relatively few cases among even presumably bipedal archosaurs — a few thecodonts, such as *Scleromochlus,* small coelurosaurs, and to a slight degree in some carnosaurs. The sharply inturned head of the femur indicates that the hind legs were carried close to and beneath the trunk and the suggestion that we are dealing with a biped is increased by the shortness of the front legs of *Lagosuchus.*

It is surprising to find so advanced a type of limb at such an early stage of the Triassic (probably Anisian in terms of the marine series). In the preceding *Cynognathus* stage of the "Eotriassic," thecodonts more advanced than proterosuchians such as *Chasmatosaurus* and *Erythrosuchus* were represented only by *Euparkeria,* as recently ably described by Ewer (1965). *Euparkeria* was advancing toward a bipedal habitus, but was still relatively primitive. One would have expected that, in the Anisian, pseudosuchians would not have advanced far beyond this level, and that forms with limbs of such an advanced sort as seen in the two types just discussed should have been characteristic only of a much later stage of the Triassic. Obviously, as these forms indicate, this assumption is incorrect. It would seem that advance and radiation among thecodonts occurred rapidly in early Triassic times; beliefs to the contrary were due to our lack of knowledge of middle Triassic faunas; study of South American forms is now bringing such faunas into the picture.

As was first clearly brought out by Krebs (1963), two distinct types of tarsal joints developed among thecodonts. In one, retained by crocodilians, the main joint between lower leg and foot lay between astragalus and calcaneum. The second type of joint is that found in dinosaurs, in which the proximal tarsals were functionally combined with the lower leg, the distal tarsals united with the foot. Both forms here described are of the second type. However, the presence of a small spur on the calcaneal region of *Lagosuchus* suggests the possibility that a transition from one type to the other may have been possible. Fusion of the two proximal elements is a condition rare even in "advanced" dinosaurs. The development of a proximal flange from the astragalo-calcaneum, seen in *Lagerpeton,* is a condition found in various theropods, but in these forms the flange is developed on the extensor rather than the flexor surface of the lower leg.

With the marked expansion of our knowledge of thecodonts that is currently taking place, classification of the group can be at best but a provisional matter, and an attempt to place the two genera just discussed in a "solid" systematic position is unjustified. It is certain that the two have no association with the series of forms which appear to have crocodilian relationships, and the tarsal construction suggests that the two are connected in some fashion with a radiation leading toward the dinosaurs and, particularly, toward the coelurosaurian group of the Saurischia.

Whether either of the two, however, can be regarded as close to the direct line leading to such dinosaurs is doubtful. *Lagerpeton* is, on the one hand, advanced in tarsal construction and, on the other, primitive or specialized in the matter of relative length of digit IV. *Lagosuchus* is more orthodox in digital construction, but precocious in astragalo-calcanear fusion, and specialized in iliac construction.

There is a classic story of the man who "mounted his horse and galloped off in all directions." The history of thecodonts, we are coming to realize, seems to have followed this pattern. We have as yet no clues as to the course followed toward birds or pterosaurs. Various thecodonts seem to have trended toward a crocodilian type of organization. The ornithischian pattern is so distinctive that at the present we can reasonably consider the Ornithischia as definitely monophyletic in origin. This is not the case with the Saurischia. The presence in the later Triassic of apparent sauropod ancestors of seemingly primitive quadrupedal nature suggests a polyphyletic origin of that order. What of the "prosauropods" of the late Triassic, the coelurosaurs, the advanced theropods of the Jurassic and Cretaceous? Quite possibly the Saurischia are a polyphyletic group that took origin from a "mixed grill" of thecodonts — a varied assemblage amongst which the two forms here described are to be included.

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